II. *On the Development of the Ovule of* Santalum album; *with some Remarks on the Phænomena of Impregnation in Plants generally.* By ARTHUR HENFREY, *Esq., F.R.S., F.L.S., Prof. of Botany in King's College, London.*

Read March 4th, 1856.

IN the 21st volume of this Society's "Transactions" are published the results of some of my earliest observations on the phænomena of fertilization and development of embryos in flowering plants. To myself, these were at that time conclusive, and they were in accordance with those published shortly before by Amici, von Mohl, and Müller, subsequently confirmed, with far more extensive illustration, by Hofmeister and Tulasne. In spite of all the adverse evidence, however, Schleiden still continues to maintain the doctrines he formerly propounded, and during the last few years he has found a most active supporter in Schacht.

Those who have not directed their labours to the practical examination of these delicate points, may feel surprise at the discrepancy existing between the statements of different observers. Those who have been engaged in the dissection of ovules in the earlier stages of development, will not much wonder at doubts arising in my mind whenever I have met with statements directly contradicting those made in my former paper. The number of instances in which a satisfactory observation is made, is very small in comparison with the number of specimens examined; and notwithstanding that I have year after year devoted much time to the dissection of ovules, these time-devouring researches have yielded me a far smaller number of facts than I could wish.

A certain amount of discrepancy exists even between the statements of the disciples of Amici, in regard to the origin of the germinal vesicle (*Keimbläschen*); and to whether it exists before, or is formed after fecundation. Hofmeister* says before; Tulasne† says he never could find it anterior to the fertilization. The latter, in the memoir just referred to (page 115), adds, "This delicate question no longer (1849) perhaps possesses all the interest which was accorded to it by MM. Mirbel and Brongniart, and more recently by Mr. A. Henfrey, in his 'Report on the Progress of Physiological Botany‡.' It is true, the existence of the embryonary vesicle at a period anterior to the arrival of the pollen-tube would, if placed beyond doubt, prove invincibly that this vesicle could not owe its origin to the latter organ; even now that the error of the pollinists is no longer uncertain, the question seems to me worthy of the attention of botanists, especially on account of the theoretical consequences involved in its solution."

Confidently as Tulasne expressed himself as to the origin of the germinal vesicle inde-

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* Entstehung der Embryo. Leipsic, 1849.   † Annal. des Sciences nat. 3^me sér. xii. p. 114.
‡ Ann. Nat. History, ser. 2. i. p. 49 (1848).

pendently of the apex of the pollen-tube, this very point is most warmly contested by Schacht[*], and notwithstanding that I have tolerably positive opinions derived from a certain number of cases, where the end of the pollen-tube and the germinal vesicle (the summit of the suspensor) were seen together, but distinct, in one preparation, the objects are so delicate, and the cause producing obscurity of the preparation so difficult to guard against, that I cannot but think the demonstration of the pre-existence of the germinal vesicle in the embryo-sac, the most important fact that can be brought forward in opposition to the views of Schleiden. As remarked by Tulasne, it has a great philosophical importance in reference to speculations as to the source of the vitality of the new being; and, as will be shown below, it is of no less importance for the establishment of the relations of the processes of embryogeny in the various classes of plants, and of the analogies which these present to phænomena attending the reproduction of animals.

As in my former paper I selected one well-established series of observations for the support of the doctrine I advocated, passing over without notice numerous fragmentary researches which, although corroborative, had in themselves nothing absolutely decisive, I shall here confine myself to the course of development of the ovule of one plant, in which the complete series of observations have been repeated many times. I feel the less hesitation in laying before the Society a paper thus restricted, from the circumstance that the example brought forward possesses features of great interest in other respects besides the main point of the fertilization. The principal facts are not indeed now brought forward for the first time, even before this Society, but they are such as few botanists have the opportunity of testing for themselves, and hence may be admitted as supplementary, partly confirmatory, partly emendatory, of the memoirs on the same subject by the late William Griffith[†].

A melancholy interest is attached to the investigations now presented; for the materials which have enabled me to repeat and control the observations of Griffith, were furnished by my lamented friend Dr. Stocks, another Fellow of this Society, suddenly cut off from us in the midst of active labours for the advancement of Indian botany.

A bottle containing a large quantity of blossoms and fruits of *Santalum album*, in all stages of growth, preserved in spirit, enabled me to trace the development of the ovules and the embryos from a very early period; the preservation in spirit seemed rather favourable than otherwise for the dissections required, since the albuminous matters were coagulated, and thus did not run out over the sections, and the cell-membranes seemed to have acquired a firmer consistence than I have usually found in fresh objects.

When very young buds are examined in vertical sections (Tab. XVII. fig. 1) the ovary is found superior, forming a conical body arising in the centre of the flower; as the bud advances in age, the adherent tube of the calyx and the side-walls of the ovary grow rapidly (Tab. XVII. figs. 3–5), so as at length to render the ovary altogether inferior (Tab. XVII. fig. 14); the original conical summit (continued into the style) becoming gradually flattened by the lateral elevation (Tab. XVIII. figs. 22, 27, 28).

The ovary never exhibits any open cavity; the centre is occupied by an elongated,

[*] Flora, 1855, p. 145; Botanische Zeitung, 1855, p. 641.
[†] Linn. Trans. xviii. pp. 59 & 71; xix. pp. 171 & 487.

conical, or rather spindle-shaped pillar, the free placenta of authors, arising from the centre of the base; the internal surface of the walls of the ovary are closely applied to the placenta, without however contracting any adherence either at the sides or above. In the youngest buds I examined (Tab. XVII. fig. 1) I found the central placenta with three cellular papillæ projecting downwards from the thickest portion, near the base, that part of the placenta below their origin being narrowed into a kind of peduncle (Tab. XVII. fig. 2). These papillæ, of cylindrical or slightly conical form, with blunt ends, pointed downward and a little outwards; they were composed of tolerably compact cellular tissue, and according to the view commonly taken of the structure of this genus, they are the nuclei of three ovules (fig. 2. *a, a*). In the youngest specimens examined, no trace of an embryo-sac could be seen, but a lighter streak (as seen by transmitted light) soon appears in the axis of each nucleus, indicating a cavity, and in a little farther advanced state a closed tubular process was found projecting from the point of each nucleus, the free extremity of a tubular embryo-sac extending internally up to the organic base of the nucleus. Examined in successive stages, the tubular embryo-sac is seen to extend downwards at first; then its external (or anterior) end (organic summit) turns outwards, next suddenly upwards over the side of the nucleus; it becomes then more and more elongated until it has grown up upon the side of the placenta so far as nearly to reach its free summit. It lies upon the outside of the placenta in the form of a slender filamentous tube (Tab. XVII. fig. 4, *b*). At the same time the posterior or internal end of the tube elongates in the substance of the placenta until it makes its way nearly to the apex. These phænomena occur in all the other (occasionally four) ovules, alike. The tubular embryo-sacs contain protoplasmic matter with a few granules, but are comparatively clear as contrasted with the cells of the nucleus, which are filled with dense protoplasm and (starch-) granules.

The next stage is the formation of a bulbous enlargement of the embryo-sac at the point where it turns up to rise over the placenta (Tab. XVII. fig. 6). The free points of the tubular sacs also contract a slight adherence to the side of the placenta near the summit, remaining free however in the greater part of their length, although closely applied to the side of the column. The protoplasmic contents next begin to increase in quantity and consistence, especially at the apex and below the bulb. A septum is soon afterwards formed at the bottom of the bulb, which, at first flat, becomes convex (looking upwards), and finally appears as an inner bulb projecting up into the cavity of the primary bulb (Tab. XVII. fig. 7). The septum divides the embryo-sac into two distinct portions; I have never discovered any cell-formation within the cavity behind (or below) the septum, either externally or internally to the nucleus. The only change this posterior (or organically inferior) part of the embryo-sac undergoes, is a tubular ramification in the substance of the placenta, to be described presently.

About the time of the formation of the septum just referred to, which is about the period of the opening of the flower, the apex of the embryo-sac becomes a little swollen (clavate), and protoplasm accumulates on it. Soon after this, before any pollen-tubes reach the placenta, from the stigma, a granular cell-nucleus, becoming gradually better defined, makes its appearance in the protoplasm of the clavate end, not quite at the extre-

mity (Tab. XVII. figs. 8 & 9, *e*).   A portion of the protoplasm in the absolute extremity (adherent to the placenta) collects into two granular masses, which become much darker-coloured than the surrounding substance, and apparently almost solid, while the closed end of the embryo-sac becomes moulded as it were on these so as to present a kind of notch or depression between them (figs. 8 & 9, *d, d*).   They lie nearly in contact, occupying (like a plug) the summit of the embryo-sac; the nucleus before mentioned being quite below them.   At this period the nucleus is devoid of a cell-membrane.

The summits of embryo-sacs, examined soon after the above period, present the ends of one or more tubes adherent to them; these tubes extend down to the embryo-sacs from the summit of the placental column; I have never traced them up the style, for this structure was so hard and resisting in my preserved specimens as not to allow of my examining the canal minutely; but there can be no doubt as to their nature.   They are the ends of pollen-tubes.   Usually one applies itself upon the very apex of the embryo-sac (Tab. XVII. figs. 10 & 11 *f*).   The tubes appear to creep down between the papillose projections of the cells of the surface of the placenta, being moulded in some degree on them; and these grooves appear to conduct the tubes to the points of the embryo-sacs, which themselves adhere to the superficial cells of the placenta; sometimes so firmly as to carry away fragments of their walls when dissected out free (Tab. XVII. figs. 9–11).

I have directed my utmost efforts to the accurate observation of the ends of the embryo-sacs with the pollen-tubes adherent.   They are tolerably easily extracted free from the ovary, with needles under a low doublet; I have examined at least five-and-twenty at various times during the last year and a half, and in the course of the observations, have applied every means to make the structures clear; mounting in water and then in glycerine, between very thin glass, so as to observe both sides; boiling in nitric acid; treating with dilute sulphuric acid alone, and with this and solution of iodine; examining the objects with a $\frac{1}{4}$ and $\frac{1}{8}$ object-glass under the compound microscope, with and without the condenser for illumination, by direct and oblique light.

The end of the pollen-tube adheres so firmly to the end of the embryo-sac, that it cannot be torn away in a really fertilized ovule.

My decided opinion is that Griffith was in error in stating that the pollen penetrates into the embryo-sac; I believe that it only applies itself firmly against it, over the point where the line of division exists between the two coagula lying on the apex of the embryo-sac, in the situation of the 'notch' above mentioned (figs. 10 & 11).   But I incline to believe that a phænomenon analogous to *conjugation* takes place.   For, as I have said, the adhesion is intimate, but the nucleus before spoken of (Tab. XVII. figs. 8 & 9 *e*) lies away from the pollen-tube, separated from it by the two coagula (*d, d*); the fissure, however, between these leads exactly from the end of the pollen-tube to the nucleus (figs. 10 & 11).   Moreover, very soon after the pollen-tube becomes adherent, the nucleus acquires a proper coat of cell-membrane,—becomes a real cell, the germinal vesicle, from which the suspensor is developed.   This cell is slightly pyriform, with an obtuse projection directed toward the fissure between the coagula (Tab. XVII. fig. 11 *g*).

I think that the pollen-tube, after becoming adherent to the summit of the embryo-sac, bursts into it, and that the contents pass into the embryo-sac, reach the nucleus, and

determine its conversion into a cell. The nucleus becomes perfectly defined, as separate from the surrounding protoplasm, just at the period of fertilization. At the same time this surrounding protoplasm (contained in a 'primordial utricle' lining the entire embryo-sac, down to the septum of the bulb (Tab. XVII. fig. 6)), becomes more dense and granular, sometimes exhibiting largish starch-granules.

Little further change occurs at the apex of the embryo-sac for some time; merely the cell-membrane enclosing the nucleus becomes thicker, and the cells assume a more elliptical form. The next step is the formation of endosperm-cells from the protoplasm of the embryo-sac. This takes place by segmentation, or free cell-formation from the whole abundant mucilaginous protoplasm, commencing always in the bulb, often advancing from them before it proceeds up the tubular part of the embryo-sac, which at first presents only a single row of 'primordial utricles' (Tab. XVII. fig. 12); the latter then divide perpendicularly (Tab. XVII. fig. 13), and the cells produced, appear to apply themselves to the side-walls and multiply for some time by free cell-formation in the centre (Tab. XVII. fig. 15). Ultimately cell-division occurs, and the whole cavity of the swollen embryo-sac being filled up with cellular tissue analogous in character to that of the nucleus,—namely, composed of squarish cells with thin walls, filled with dense protoplasm, containing increasing quantities of minute starch-granules,—the *albumen* of the end becomes a distinct structure, on the surface of which all trace of the originally bounding embryo-sac is soon lost (Tab. XVII. fig. 16).

The first change in the germinal vesicle is its elongation downwards into a cylindrical form; then cross septa appear (Tab. XVII. fig. 15 *g*, Tab. XVIII. fig. 19 *g*) one after another, so that it is converted into a short row of cells. The uppermost remains appressed to the coagula in the apex of the embryo-sac, and does not appear to become developed further; forming a kind of suspensor. The lower cells multiply greatly (Tab. XVIII. fig. 23) and form an elongated, clavate cellular body, the embryo, in which at first no trace of regions can be detected,—only a greater density of the tissue and abundance of granular contents at the cotyledonary (inferior) extremity (Tab. XVIII. figs. 22 & 24 *g*, fig. 25).

The conditions of the walls of the ovary during these changes deserve some attention; the outer substance of the young fruit is formed of a firm layer of tolerably equal thickness all over, constituting what we may call the epicarp together with the mesocarp (Tab. XVIII. figs. 27 & 28 *s*). These define and correspond to the outward form of the fruit. The portion immediately beneath the epidermis is composed of oblong cells with their longest dimension in the direction of the axis of the fruit; these pass insensibly into a denser layer of closely-packed polygonal cells with thick walls. These two regions are coloured, while the endocarp is nearly colourless (Tab. XVIII. figs. 27 & 28). The cells of the mesocarp (well defined internally to the naked eye) appear, under the microscope, to pass again insensibly into the soft endocarp (figs. 27 & 28 *r*), composed of membranous, globular, and polygonal cells, loosely packed, of much greater diameter, for the most part, than those of the mesocarp. The endocarp (figs. 27 & 28 *r*) fills up the whole space between the dark rind of the fruit (*s*) and the placenta (and ovules) (*o*, *p*), during the earlier expansion of the ovary. Where in contact with the embryo-sacs and placenta, it is of denser texture and of darker colour, having a definite, separable boundary. A perpendi-

cular line is seen leading from the apex of the placenta to the point corresponding to the base of the style; the cells of the endocarp exhibit a radiating linear arrangement on the upper half, the lines running upwards and outwards from the placenta (fig. 27).

A remarkable phænomenon occurs meanwhile in the interior of the placenta. It has been stated that there is never any appearance of development of cells in that part of the embryo-sac, behind (or below) the septum formed a little way outside the nucleus Tab. XVII. figs. 7–12). The inner bulbous expansion, formed by the septum itself, which becomes convex, and protruded upwards into the centre of the larger bulb, is found in the same condition, as long as the structures are traceable, and it finally forms a kind of stalk or "funiculus" to the seed, inserted into the substance of the albumen (Tab. XVII. figs. 12, 17, and Tab. XVIII. fig. 26), and connecting this with the remains of the placental structure. I have already mentioned, that while the tubular prolongation of the embryo-sac, outside the nucleus, is growing up over the placenta, the posterior end, inside the nucleus, also grows up, breaking down the tissue before it, into the substance of the placenta (Tab. XVII. fig. 4). Within this organ it proceeds nearly to the summit, and then turns round somewhat suddenly, and grows down again, with various ramifications, in the centre of the placenta, and even into the receptacle below where these arise (Tab. XVIII. figs. 20, 21): I have never seen anything like cell-formation, or even production of septa in these posterior branches of the embryo-sac; they contain a granular protoplasmic substance, which, in my preserved specimens, is of a red colour. The ends of the barren embryo-sacs undergo the same kind of development within the placenta, although the changes in the external portion cease at the period of the formation of the germinal vesicle. The ramifications of the three distinct embryo-sacs become somewhat interlaced, but I have never certainly detected any conjunction or adhesion of them, as suspected by Griffith.

It remains only to notice the further changes exhibited by the ovule. The endosperm or albumen of the embryo-sac increases enormously in quantity, so as to expand the sac in all directions (Tab. XVIII. figs. 16, 20, 26); the placenta is broken off just below the point of origin of the ovules (fig. 26), and pushed outwards and upwards by the enlargement of the albumen (Tab. XVIII. figs. 27, 28 p); in the ripe fruit it is found lying upon the surface of the latter (Tab. XVIII. figs. 30 & 32 p), which, through the displacement and destruction of the endocarp, is finally in immediate contact with the woody mesocarp. On examining the remnant of the placenta, even in the ripe fruit, it is found to be connected with the endosperm by the bulb. When the placenta is then broken away from the receptacle, and pushed up, the receptacle upon which it was seated is also carried away towards the same side of the albumen, on the outside of which, near the base, it is ultimately found (Tab. XVIII. figs. 28, 30, 32 v) as a little mass of sphacelated tissue overlying a pit or foramen, which leads to an internal dark line, running through the endosperm to the cotyledonary extremity of the embryo (Tab. XVIII. fig. 30 v). In this line, and in the sphacelated mass, are found remains of the posterior ramified processes of the embryo-sac, some of which are also found attached to the upper fragment or placenta*. In the ripe seed, the embryo is found lying a little out of the axis of the albumen, in a

* This seems to resemble what Mr. Bentham describes in *Olacaceæ*, Linn. Trans. xviii. p. 675.

vertical position (fig. 33), or with the cotyledons curved a little towards the lateral basilar scar just mentioned (fig. 35). The radicle is at the upper end of the seed and terminates in an acute apiculus (Tab. XVIII. figs. 34 & 36).

In the mature fruit the mesocarp forms a hard shell, outside which the epicarp forms a thin layer of pulpy substance (Tab. XVIII. fig. 22). The woody shell is slightly pointed and trigonal above, presenting three converging ridges (Tab. XVIII. fig. 31) when the epicarp is removed. Within the woody mesocarp the albumen or endosperm of the seed lies free; the coat formed by the embryo-sac is no longer distinguishable, but the endosperm is covered with brownish membranous scales (Tab. XVIII. fig. 32), composed of compressed withered fragments of the lax cellular tissue of the obliterated parenchymatous endocarp.

The above observations confirm in almost every respect those published by Griffith in the Transactions of the Linnean Society, the main point of difference lying in the statements made with respect to the phænomena presented at the summit of the embryo-sac at the time of fertilization; in which my account is strongly opposed to those given by that author, not only in *Santalum*, but in *Osyris* and the *Loranthaceæ*. Notwithstanding the high value I attribute to Griffith's labours, increased and confirmed by the researches now brought forward, I feel very confident of the correctness of the account I have given of the origin of the embryo from a pre-existing germ, and I have little doubt that the process of fecundation is such as I have described in *Osyris*, and the other cases. The importance attaching to the truth of the view I have propounded will be farther illustrated below.

Every one who has studied the development of the ovules of *Santalum*, and the allied genera, has been struck by the remarkable anomalies which present themselves. The entire protrusion of all the (apparently) essential part of the embryo-sac from the apex of the nucleus, the development of the endosperm in the external compartment of the sac, altogether independently of the nucleus, are very remarkable; while the posterior development of the embryo-sac is no less singular. The idea has been suggested that the entire central body here described as a free placenta with the ovules reduced to nuclei, might be one ovule with three embryo-sacs; and also that the central body is all placenta, the nuclei being merely the funiculi of ovules reduced to embryo-sacs. There does not seem to be sufficient ground for either of these assumptions, although the former is in some respects plausible.

The principal reason which could be advanced in favour of the second idea, is the apparently abnormal position of the embryo, the cotyledonary extremity of which is next the apex of the nucleus, and the radicle end pointing in the direction of the base of the nucleus. But this is rather an apparent than a real irregularity. It would be a pedantic insistence upon terms to call that end of the embryo-sac engaged in the apex of the nucleus, the micropyle-end; it is really the middle, and the embryo-sac is in fact campylotropous, its organic base or chalazal end being in the interior of the nucleus, while the micropyle-end is prolonged out beyond the micropyle, and turned up so as to lie (outside) against the chalazal end.

In regard to the first of the two views above referred to, the only circumstances which

it appears to me can be urged in favour of the idea that the central body is not a placenta, but a compound nucleus with three embryo-sacs, are as follows :—

The central body is stated by Griffith to form at first, in *Osyris*, but a slightly-elevated cone with three (or four) papillæ (or nuclei) at its sides. In the youngest specimens of *Santalum* I examined, the placenta was highly developed as a pillar in the centre of the ovary (Tab. XVII. figs. 1 & 2). The papillæ might be either three points of one ovule, or three nuclei with three chalazal ends blended in the centre, and the growing-up of the central column, which goes on for a certain time after the embryo-sacs are distinguishable, might be regarded as a conversion of the compound ovule, or the three conjoined ovules, into an anatropous structure, the chalazal end being at the apex of the conical mass, the micropyles free and turned down next the "funiculus." The subsequent retroversion of the embryo-sacs would still be anomalous, connected however in some degree, through *Osyris*, *Avicennia** and *Myzodendron*† (in which the embryo-sac is not extended unless fertilized) with the ordinary conditions. Then the growth of the posterior ends of the embryo-sacs would seem to represent a kind of chalazal structure, connecting them below in a kind of central raphe with the peduncular placenta. The relative positions of the remains of the nuclei and the central body, and of the remains of the peduncle of the placenta, in the ripe fruit, would then indicate a rupture at the umbilicus, which was carried up to near the top of one side of the seed, while the funiculus was driven outwards on the same side, and almost obliterated‡.

Some degree of likelihood attaches to the explanation just given when the *Santalaceæ* are compared with the *Loranthaceæ*, with which they appear to be nearly connected through *Myzodendron* (which genus is nearer the former than the latter family as regards ovulary structure§). In the *Loranthaceæ* the supposed compound, triple ovule, being atropous instead of anatropous, would naturally be still more completely combined into one piece; it would here be almost a question of words whether there were confluent nuclei or one nucleus with three parallel embryo-sacs. Then the phenomena observed in *Loranthus* might afford a still farther confirmation, as indicating analogy with the *Coniferæ*, in which the existence of a number of (secondary) embryo-sacs is the rule.

These points deserve further attention, and can only be elucidated by the study of the development in more of the genera of these remarkable families. I should not omit to mention here the observations of DeCaisne on *Thesium*‖, which I have not yet repeated, but which agree essentially with the statements respecting *Santalum* made by Griffith and myself.

The reason which perhaps most of all induced me to present these observations to the notice of the Society, is the remarkable analogy which is shown to exist between the phenomena of fecundation above described, and those which have recently been demon-

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* Griffith, Linn. Trans. xx. p. 1.

† Hofmeister, in Grisebach, üb. Philippi und Lechler's Pflanzensamml. Abhandl. Götting. Gesellsch. 1854.

‡ In *Santalum* no vascular cords can be distinguished in the conical placenta ; in *Avicennia*, according to Griffith, (*l. c.*) the vascular cord reaches nearly to the base of the embryo-sac, so that the chalazal end of the ovule is marked.

§ R. Brown, Linn. Trans. xix. p. 231 ; Hofmeister, *l. c.*

‖ Ann. des Sciences nat. 2^{me} sér. xiii. p. 300.

strated to take place in some of the lower plants. I pass over the numerous discoveries that have been made of late years in the higher *Cryptogamia*, from the *Marsileaceæ* to the *Liverworts*, showing the pre-existence of a germ, and its fertilization by spermatozoids. I may refer to my own publications on this subject elsewhere*. The cases most immediately interesting to me in this instance are those described by Thuret in the *Fucaceæ*, already repeated by Pringsheim, and the researches of the latter and of Cohn on certain filamentous Confervoids. According to the elaborate investigations of Thuret† the spores of *Fucus* are discharged from the spore-sacs as globules of protoplasmic substance, bounded by the structure denominated by Von Mohl the primordial utricle, without a cellulose coat. While swimming free in the water, spermatozoids come in contact with them in large numbers, and after a certain time a cellulose coat is developed upon the surface of the spore; the latter thus becomes encysted, and forms a true cell, which then germinates, to produce a new plant. Pringsheim‡ describes essentially analogous phenomena as occurring (inside the parent-cells) in *Vaucheria*, and Cohn's§ account of the fecundation of the spores of *Sphæroplea* also agrees with these.

These facts, together with those I have brought forward in this paper, tend to prove that the process of impregnation in plants consists in the absolute admixture of the protoplasmic substance of two cells ("male" and "female"); of which the female (or germinal) substance or body always pre-exists in the form of a nucleus or "protoplast," while the male (or spermatic) substance exists in the form of a granulose fluid. In the Flowering Plants the spermatic fluid is conveyed directly into the embryo-sac by the channel of the pollen-tube; a similar process appears to exist in the *conjugation* of the lower *Algæ*; in other cases the spermatic fluid is conveyed from organs situated at a distance from the parent-cell of the germinal vesicle, by the agency of locomotive structures (spermatozoids) developed in the spermatic cells, bathed in and discharged with their contents, and themselves composed of the nitrogenous protoplasmic matter of cell-contents.

In my Memoir on *Orchis Morio*‖, I described the nascent germinal vesicles as cells. Hofmeister and others in like manner call them cells; but comparison of my older drawings and those of Hofmeister with new observations, leads me to believe that, on careful examination, these bodies will be found to consist of nuclei or "protoplasts" before fertilization¶. I may note in reference to this, that I have already some confirmation from another case besides *Santalum*, and I trust to bring forward hereafter more complete evidence on the subject.

Jan. 30, 1856.

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* Report of the British Association, 1851; Annals of Natural History, 2 ser. ix. p. 441; Linnean Transactions, xxi. p. 117.

† Ann. des Sciences nat. 4 ͤ sér. ii. p. 197.   ‡ Bericht Berlin Akad. March 1855.

§ Bericht Berlin Akad. May 1855.   ‖ Linn. Trans. xxi. p. 7.

¶ Certain circumstances which I observed in the *archegonia* of the Ferns, also afford good reasons for inquiring whether the parent-cell of the germinal vesicle is not open at a certain period there, offering a passage for the spermatozoids to a naked nucleus. See especially the figures 56, 57, 63–70 of plate 16 in my Memoir on the Development of Ferns (Linn. Trans. xxi. p. 117).

EXPLANATION OF THE PLATES.

The figures magnified 50 diameters and upward were drawn by the aid of the *camera lucida*.

TAB. XVII.

Fig. 1. Vertical section of the ovary of an unopened bud.

Fig. 2. Placenta with two nuclei (*a a*) from the same.

Fig. 3. Vertical section of the ovary, &c., of a flower just opened.

Fig. 4. Placenta of the same with two nuclei (*a, a*) and one embryo-sac (*b*).

Fig. 5. Section of an ovary somewhat older.

Fig. 6. Nucleus (*a*), embryo-sac (*b*) with germinal vesicle and pollen-tubes at the apex; from fig. 5. septum of the bulb not yet developed.

Fig. 7. Point of a nucleus and the embryo-sac (*b*), with a fully-developed septum in the bulb (*c*).

Fig. 8. Apex and unimpregnated embryo-sac, with terminal coagula (*d d*) and a nucleus (*e*).

Fig. 9. Another more advanced.

Fig. 10. Another with a pollen-tube (*f*) applied.

Fig. 11. Another when the nucleus (*e*) is converted into a cell with a cellulose wall (*g*).

Fig. 12. Part of an impregnated embryo-sac (*b*) attached to its nucleus (*a*), with endosperm-cells formed in it.

Fig. 13. Upper end of another one with the endosperm more developed.

Fig. 14. Vertical section of an ovary some time after impregnation.

Fig. 15. Upper end of the endosperm of an ovule from fig. 14, with the germinal vesicle (*g*) undergoing division.

Fig. 16. A less advanced ovule, with the endosperm considerably developed; the dotted line runs to the point of insertion of the inner bulb (fig. 17) formed by the septum.

Fig. 17. The inner bulb (similar to that in figs. 7 & 12) drawn out from the endosperm of fig. 16; *a*, nucleus.

Fig. 18. Inner bulb drawn out from another endosperm.

TAB. XVIII.

Fig. 19. Apex of a young ovule with the embryo (*g*) dividing into four cells; *i*, endosperm cells.

Fig. 20. Placenta and ovules, one fertile, the other barren, of a more advanced ovary; the future prolongations of the embryo-sacs are seen in the placenta: lettering as before.

Fig. 21. Posterior prolongations of an embryo-sac partly dissected out.

Fig. 22. Section of an imperfect fruit.

Fig. 23. Apex of the ovule of fig. 22, with embryo (*g*); *d d*. coagula; *k*. upper cell of the row formed from the germinal vesicle (*suspensor*).

Fig. 24. Upper point of a more advanced ovule, with the embryo (*g*). The small figure on the left is a section of the ovary from which it was taken, nat. size.

Fig. 25. Embryo from fig. 24.

Fig. 26. Placenta and ovule of a fruit nearly as in fig. 27, the placenta *p*. already torn away from the receptacle: lettering as before.

Fig. 27. An immature fruit; *o.* ovule, on the side of which lies the placenta *p*; *r.* endocarp; *s.* rind composed of the blended mesocarp and epicarp; *v.* peduncle of the placenta.

Fig. 28. Another, more advanced; lettering as before.

Fig. 29. A fruit nearly ripe; part of the succulent epicarp removed, laying bare the shell or mesocarp *s.*

Fig. 30. Section of fig. 29: letters as before; *p.* & *s.* are the sphacelated placenta (*p*), and its base (*v*) removed from the points indicated by the dotted lines. The endocarp is now obliterated.

Fig. 31. Ripe fruit with the pulp removed from the shell.

Fig. 32. The seed of the same with the shell or mesocarp removed; *r.* scaly fragments of the obliterated endocarp; *p.* placenta; *v.* its original base.

Fig. 33. Section of fig. 32 with the embryo (*g*) in the albumen *v.*

Fig. 34. Embryo extracted.

Fig. 35. Section of another seed.

Fig. 36. Its embryo extracted.